

Evolution of Labral Spines in *Acanthais*, New Genus, and Other Rapanine Muricid Gastropods

by

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Abstract. The new genus *Acanthais* is proposed for *Acanthina brevidentata* (Wood, 1828), a rapanine muricid gastropod common on tropical eastern Pacific rocky shores. It is distinguished by the presence of a labral spine, a central fold on the columella, and other characters of the shell and radula. *Acanthais* is one of at least five members of the Rapaninae in which a labral spine has evolved independently. This feature is an exaggeration of an enlarged ventrally projecting crenation at the base of the outer lip. Such crenations are widespread in the Rapaninae. Biogeographically, *Acanthais* is one of at least eight endemic tropical eastern Pacific genera of gastropods with an origin during or after the Pliocene.

INTRODUCTION

Acanthina brevidentata (Wood, 1828) is a common intertidal muricid gastropod in the tropical eastern Pacific (Keen, 1971), belonging to the Rapaninae (Thaidinae of authors; see Kool, 1993b). Because of the presence of a labral spine (a ventrally projecting spine near the base of the outer lip), the species has usually been assigned to the ocenebrine muricid genus *Acanthina*. Cooke (1918), Wu (1985), and Vermeij (1993) realized that this assignment is incorrect, but did not provide a more suitable taxonomic placement. Here we erect the new genus *Acanthais* to accommodate the species. We also take the opportunity to comment on the evolution of labral spines among Rapaninae and on the biogeographical distinctness of a number of rocky-shore gastropod genera in the tropical eastern Pacific.

MATERIALS AND METHODS

All specimens used in the analysis of teleoconch characters are housed in the Vermeij collection. Fifteen lots of *Acanthina brevidentata* spanning a geographical range from northwestern Costa Rica to southern Ecuador were examined. Characters of shell microstructure, operculum, radula, and anatomy were assessed in six male and six female specimens of *A. brevidentata* from Venado Island,

Panama (MCZ Number 298408). J. H. McLean of the Los Angeles County Museum kindly supplied us with specimens on which the protoconch was preserved (LACM 70-65.29, Playa del Coco, Costa Rica). For methods of dissecting protocol and preparation for SEM photography of the radula, protoconch, and shell microstructure, see Kool (1993b).

Throughout the text, generic names are used in the narrow sense unless otherwise indicated, and the names of type species are those currently accepted rather than the names originally designated.

SYSTEMATICS

Family MURICIDAE Rafinesque, 1815

Subfamily RAPANINAE Gray, 1853

Genus *Acanthais* Vermeij & Kool, gen. nov.

Type species: *Acanthais brevidentata* (Wood, 1828).

Diagnosis: Rapanine with a teleoconch sculpture of spiral cords, up to five on body whorl, bearing low rounded nodes, the two adapical cords often obsolete or missing; secondary sculpture of exceedingly fine spiral threads; outer lip bearing short labral spine adapical to fifth major spiral cord;

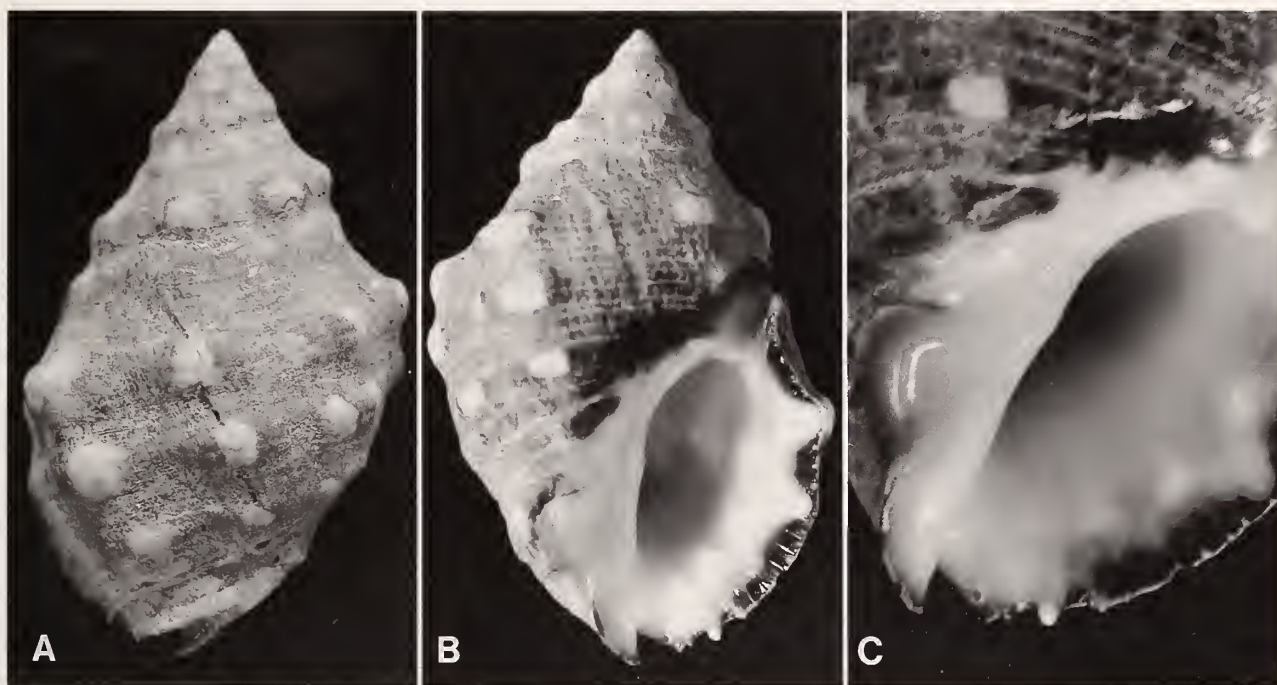


Figure 1

Shell morphology, *Acanthais brevidentata* Vermeij & Kool, gen. nov., Isla Taboga, Panama, collected 25 February 1986. A. dorsal view, $\times 3$. B. apertural view, $\times 3$. C. basal portion of outer lip, $\times 3$.

inner surface of outer lip denticulate, without lirae; columella straight, bearing distinct central fold that extends into aperture.

Acanthais brevidentata (Wood, 1828)

(Figure 1)

Buccinum brevidentatum Wood, 1828:12.

Monoceros brevidentata Wood, 1828:43.

Description: *Protoconch*. Moderately tall, of about 3.5 adpressed whorls (exact count could not be made from available specimen), and with well-developed outward-flaring lip and sinuigeral notch (Figure 2). Angular, ridged shoulder on last 1.5 whorls. Series of vertical plicae on area close to end of last whorl. Subsutural plicae on last 2.5 whorls. Increasingly well developed ridged shoulder with subsutural plicae. Last whorl with small pustules and with vertical plicae on last quarter whorl.

Shell Morphology. Shell moderately high-spired (apical half-angle of spire 30° to 36°), sutures between teleoconch whorls distinct; umbilical slit absent; siphonal canal short, broad, forming upturned notch at basal end, and set off from remainder of last whorl by prominent fasciole. Teleoconch whorls sculptured by major nodose spiral cords and by numerous exceedingly fine spiral threads; on last whorl up to five primary cords, one at the suture, two central

ones with prominent low rounded nodes, and two subordinate basal cords of which one (the most basal cord) is often missing. Outer lip crenate at edge, bearing short, sharp labral spine at position basal to abapical (fifth) primary spiral cord and situated at the end of a shallow external groove. Inner edge of outer lip with four weakly elongate denticles situated close to the edge of the lip; inner surface of outer lip otherwise smooth, not lirate. Adapical end of aperture constructed by prominent parietal rib; no anal slit. Columella straight, with more or less distinct central fold extending into the aperture and one or more weak basal riblets that are confined to the ventral surface of the inner lip.

Shell Microstructure. Inner layer of aragonite with crystals oriented in a 45-degree angle to the growing edge (Figure 3A); middle layer of aragonite with crystals oriented perpendicular to growing edge; outer layer of aragonite with crystal planes oriented parallel to growing edge. Inner layer absent in some specimens.

Operculum. D-shaped, but upper end more rounded, with lateral nucleus in center right. Free surface with bracket-shaped growth lines; attached surface with 3–4 bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy. The anatomy of *Acanthais brevidentata* is typically rapanine, and schematic drawings of anatomical features, as well as detailed explanations of terminology used,

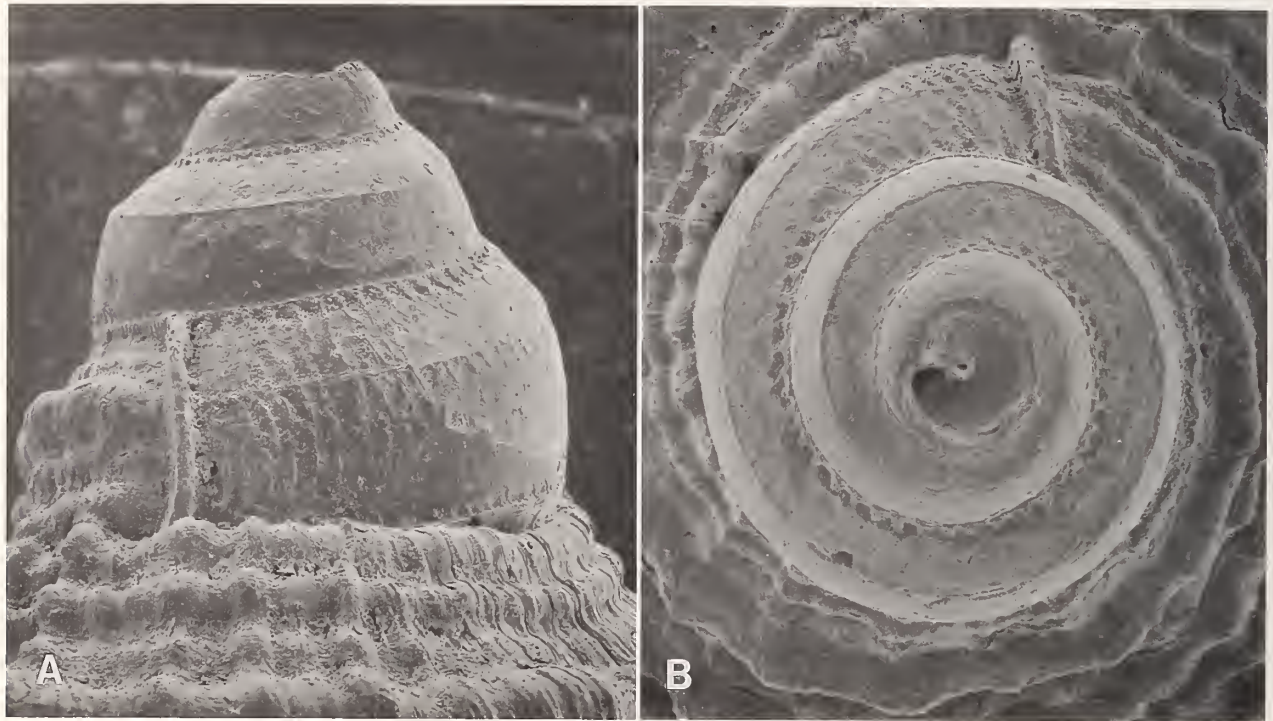


Figure 2

Protoconch, *Acanthais brevidentata* Vermeij & Kool, gen. nov., Playa del Coco, Costa Rica, LACM 70-65.29. A. lateral view, $\times 80$. B. apical view, $\times 80$.

can be found in previous papers by Kool (1989, 1993a, b). It should be noted that coloration given for the anatomical features described below is found in the living animals and may have faded or disappeared following preservation in alcohol.

Head and foot. Foot flecked with grey, black, and orange; edge primarily orange with minute white specks; sole opaque grey. Cephalic tentacles elongate, thin, dark brown with grey tips. Incurrent siphon with white and orange specks proximally, flecked with black distally. Accessory boring organ elongate, well developed; in females dorsal to short ventral pedal gland.

Mantle cavity. Osphradium about two-thirds of ctenidial length, equal in width to ctenidium. Right pecten wider than left. Each lamella (12-15/mm) attached to mantle roof along one-half its length. Anteriormost portion of ctenidium curving around anterior osphradium. Ctenidial lamellae (14-17/mm) with strongly convex lateral edges, more wide than high anteriorly, more high than wide posteriorly. Supporting rods extending beyond lateral edge of each lamella, forming small papilla.

Female reproductive system. Vaginal opening inconspicuous, starting with small fold onto rectum, continuing as minute duct without obvious area for sperm storage. Small, looped flange creating ventral channel, located under small ventral lobe anteriorly, in lower center between

left and right lobes posteriorly. Ventral lobe small anteriorly, increasing in size toward posterior, until disappearing completely posteriorly. Ingesting gland dark green to black, partially located on left side of posterior capsule gland and albumen gland, extending to kidney. Ingesting gland consisting of many smaller compartments filled with dark brown material. Albumen gland omega-shaped with several posterior seminal receptacles on dorsal side entering into gland (see Kool, 1988). Albumen gland anteriorly opening into ovi-sperm duct, posteriorly into oviduct. Ovary golden yellow. Minute, papillalike pseudopenis present in most females examined.

Male reproductive system. Penis small (slightly larger than tentacle), sinuous, flattened dorso-ventrally, elliptical in cross-section, gradually tapering, almost transparent, grey opaque. Penial vas deferens a duct-within-a-duct (Kool, 1988:fig. 3B), located toward anterior and dorsally. Cephalic vas deferens minute, poorly developed. Prostate gland orange-golden from outside, with spongy texture and with one or two poorly developed ducts. Posterior vas deferens well developed, dark brown.

Alimentary system. Paired accessory salivary glands thin, short (one-ninth shell height); left gland adjacent to left salivary gland; right gland loose from right salivary gland. Salivary glands overlying short, pear-shaped valve of Leiblein. Salivary ducts attached to esophagus directly ante-

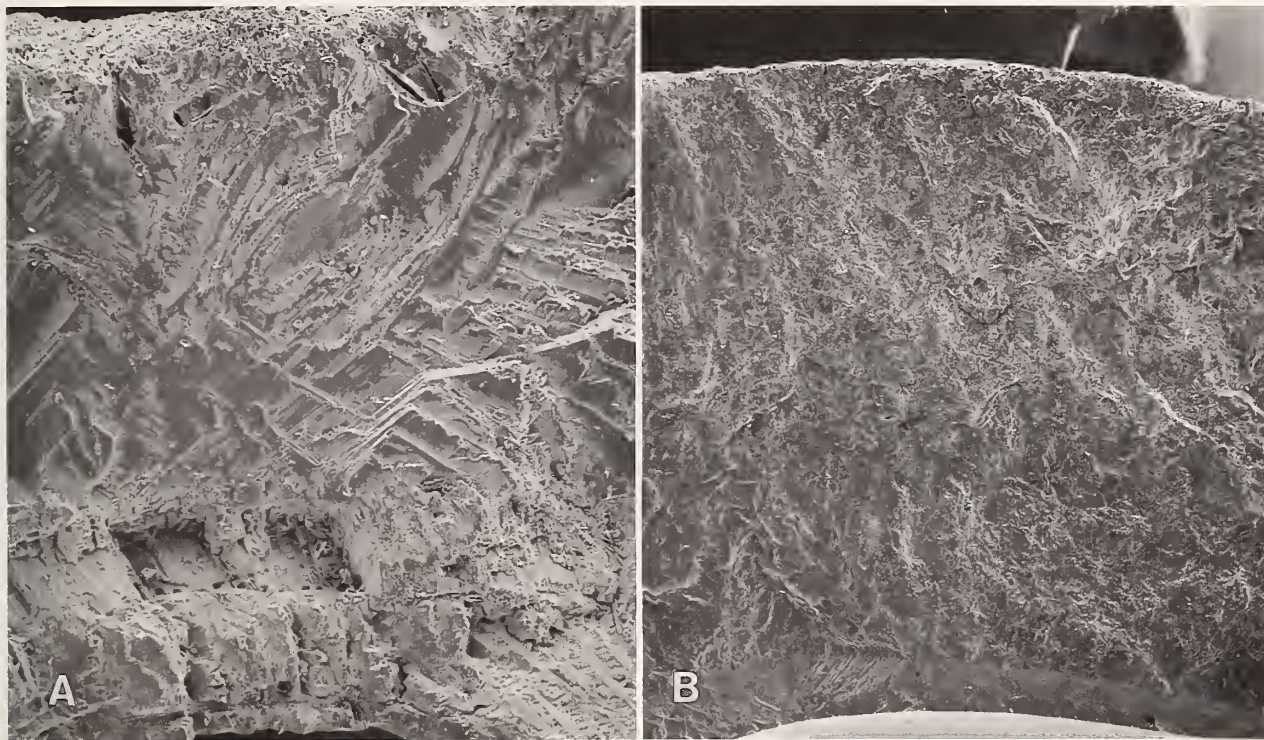


Figure 3

Shell microstructure. A. *Acanthais brevidentata* Vermeij & Kool, gen. nov., Venado Island, Panama, MCZ 298408, $\times 50$. B. *Acanthina unicornis*, Talcahuano, Chile, MCZ 3717, $\times 30$.

rior to valve of Leiblein. Glandular folds in mid-esophageal region not visible. Connection between mid-esophagus and gland of Leiblein poorly developed, very short. Posterior esophagus attached to gland of Leiblein by connective tissue. Gland of Leiblein with thick strawlike membrane obscuring spiral nature of gland. Posterior duct longer than one-half length of gland of Leiblein, emptying into dorsal branch of the afferent renal vein. Stomach a widened tube, with many small folds on posterior mixing area, oriented toward center. Stomach typhlosole and intestinal typhlosole well developed. Two digestive diverticula present. Digestive gland dark yellow to light brown. Rectal gland wide, dark green, along two-thirds of capsule gland in females, along three-fourths of prostate gland in males.

Radula. Ribbon length 30–35% of shell height. Central cusp of rachidian wide, flame-shaped; inner lateral denticle low on base of lateral cusp; outer edge of lateral cusp with one denticle (in some specimens only a remnant); marginal area with two marginal denticles and well-developed marginal denticle (Figure 4A). Lateral teeth nearly equal to width of rachidian tooth (Figure 4B).

Comparative remarks: *Protoconch*. The protoconch is typically rapanine; it is multispiral with 3+ whorls (exact figure cannot be given due to imperfect preservation of

protoconch specimen) as opposed to the typical paucispiral protoconch in ocenebrines of 1.5 whorls; and the outward-flaring lip and sinusigeral notch are indicative of a planktotrophic larval stage, found in all rapanines and absent in ocenebrines. The *Acanthais* protoconch is similar to that of *Stramonita* in both overall shape and sculptural pattern.

Shell Morphology. *Acanthais* bears a strong superficial resemblance to three ocenebrine genera, *Acanthina* Fischer von Waldheim, 1807 (type species: *A. monodon* (Pallas, 1774), southern South America); *Acanthinucella* Cooke, 1918 (type species: *A. punctulata* (Sowerby, 1835), California); and *Spinucella* Vermeij, 1993 (type species: *S. tetragona* (Sowerby, 1825), Pliocene, North Sea Basin). All four genera possess a labral spine and strong spiral cords. *Acanthais* differs from members of the Ocenebrinae by columellar, apertural, and sculptural characters.

Like many Rapaninae, *Acanthais* has sculpture on the columella. In *Acanthais*, there is a central fold. This fold is much weaker than the central fold of *Cymia* Mörch, 1860 (type species: *C. tecta* (Wood, 1828), tropical eastern Pacific). The latter genus differs widely from *Acanthais* in its lirate aperture, fine spiral ribs, adapical apertural notch, and strong peripheral tubercles. Ocenebrines have a smooth columella. Some rapanines also have a smooth

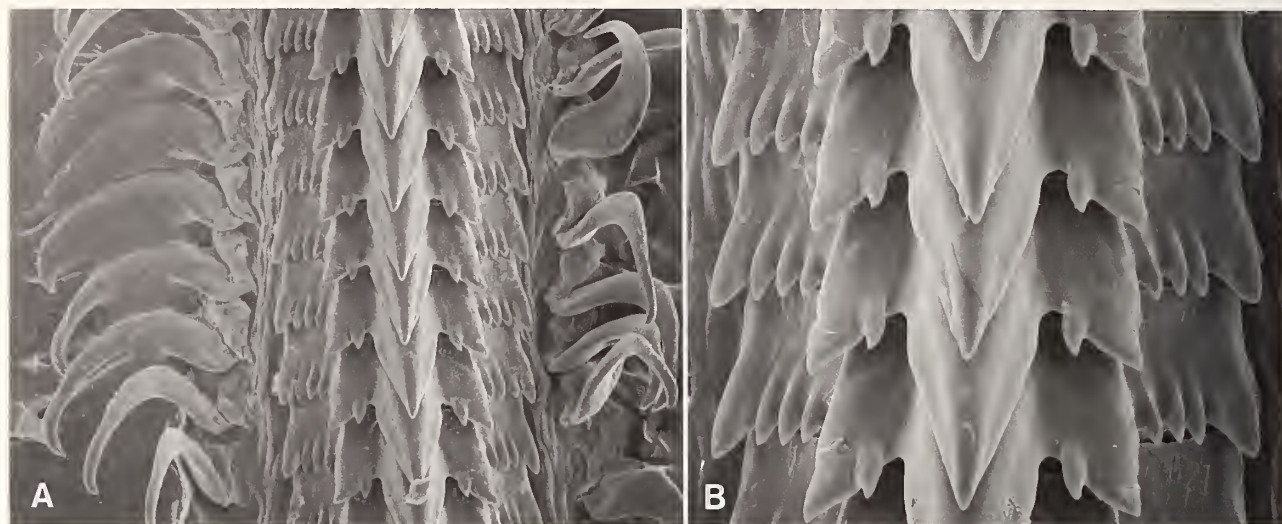


Figure 4

Radula, *Acanthais brevidentata* Vermeij & Kool, gen. nov., Playa del Coco, Costa Rica, LACM 70-65.29. A. $\times 450$. B. rachidian tooth, $\times 1000$.

columella. These include *Concholepas* Lamarck, 1801 (type species: *C. concholepas* (Bruguière, 1789), western South America); *Rapana* Schumacher, 1817 (type species: *R. bezoar* (Linnaeus, 1758), Indo-Pacific); *Ecphora* Conrad, 1843 (type species: *E. quadricostata* (Say, 1824), Pliocene of Virginia); and limpetlike morphs of *Plicopurpura* Cossmann, 1903 (type species: *P. columellaris* (Lamarck, 1816), tropical eastern Pacific). These taxa are low-spired to limpetlike, and have a sculptural pattern different from that of *Acanthais* and related genera.

In *Acanthais*, there is a parietal rib that terminates as a distinct knob at the apical end of the aperture. This feature is absent in most Ocenebrinae, including *Acanthina* and *Spinucella*. Some species of *Acanthinucella* and many populations of *Nucella emarginata* (Deshayes, 1839) from California possess a parietal tubercle, but this feature is discrete and is not a spiral parietal rib as it is in *Acanthais* and most other Rapaninae. A similar parietal rib occurs in members of Muricinae.

The five-rib pattern of major spiral cords on the body whorl sets *Acanthais* apart from Ocenebrinae but links it to many members of the Rapaninae. The adapical cord, or subsutural ridge, lies just below the suture and periodically forms apically directed extensions that produce weak knobs. At the outer lip, the most recently formed of these extensions produces a gutterlike extension with the opposing terminus of the parietal rib. The subsutural cord and corresponding posterior apertural gutter are found in nearly all Rapaninae but are lacking in *Acanthina*, *Acanthinucella*, *Spinucella*, and other Ocenebrinae. Most ocenebrines have seven or more primary spiral cords. Mem-

bers of the *Acanthinucella lugubris* (Sowerby, 1821) group from northwest Mexico (see Wu, 1985) have only four primary spiral cords, the two apical ones bearing nodes and the two basal cords being broadly rounded and set close together. Recent specimens of the *Nucella emarginata* species complex have five major cords, but there is no subsutural cord as in Rapaninae.

Among rapanine genera, *Acanthais* bears a strong superficial resemblance to *Stramonita* Schumacher, 1817 (type species: *S. haemastoma* (Linnaeus, 1767), Mediterranean and West Africa). In both genera, cords 2 and 3 on the body whorl (counting from the suture) are adorned with a row of equally prominent nodes. The primary cords of *Stramonita*, however, are narrow and angular, whereas those of *Acanthais* are low, broad, and round-topped. Moreover, the two genera differ in secondary spiral sculpture and in the way that the primary cords are reduced in many populations. In *Acanthais*, cord 5 (the most basal one) is rarely expressed, so that the primary sculpture appears to consist of three closely spaced cords on the central portion of the body whorl and a very weak noded subsutural cord. The entire shell surface is overlain by extremely fine spiral threads. In populations of *Stramonita* in which the primary spiral cords are reduced, the primary cords are of the same size as, and are difficult to distinguish from, the relatively coarse secondary cords or riblets. This is especially so in western Atlantic populations of *S. haemastoma* (belonging to the subspecies *floridana* Conrad, 1837, and *canaliculata* Gray, 1839), in the eastern Pacific *S. biserialis* (Blainville, 1832; Figure 1D-F), and in the Peruvian *S. delessertiana* (Orbigny, 1941). These typical

species of *Stramonita* also differ from *Acanthais* by the presence of riblets (lirae) on the inner side of the outer lip. Lirae are absent in *Acanthais*. Moreover, typical species of *Stramonita* lack the central columellar fold of *Acanthais*, and also lack a labral spine.

The tropical eastern Pacific genus *Neorapana* Cooke, 1918 (type species: *N. muricata* (Broderip, 1832)) resembles *Acanthais* in possessing a short labral spine in a position just basal to cord 5. In shell characters, *Neorapana* differs from *Acanthais* by lacking the central columellar fold, by having the inner side of the outer lip lirated rather than smooth, and by possessing an umbilical slit.

Several Indo-West-Pacific rapanines are also superficially similar to *Acanthais*. *Thais aculeata* (Deshayes & Milne Edwards, 1844) is the type of *Thalessa* H. & A. Adams, 1853, but was assigned to *Stramonita* by Fujioka (1985) on the basis of radular characters and to *Mancinella* Link, 1807 (type species: *M. alouina* (Röding, 1798), tropical Indo-Pacific) by Tröndle & Houart (1992). This species and its relatives have a weak to obsolete central columellar fold and, like *Acanthais*, a nonlirate outer lip bearing denticles on its inner side. However, whereas it is the fifth (most basal) primary spiral cord that is often missing in *Acanthais*, the fourth cord is usually weakest in the *T. aculeata* group. Strong erect spines adorn all five cords or all but the fourth cord in *Thalessa*. The coarse secondary spiral sculpture of *Thalessa* resembles that of *Stramonita* rather than the fine threads of *Mancinella* or *Acanthais*. It may be that *Thalessa* is close to *Stramonita*, but further anatomical study is needed to clarify the placement of this group.

Finally, *Acanthais* shares many features with *Thais* Röding, 1798 (type species: *T. nodosa* (Linnaeus, 1758), tropical West Africa). Species of *Thais* resemble *Acanthais* in having exceedingly fine secondary spiral sculpture and in lacking lirae on the inner side of the outer lip, but they lack a central columellar fold and a labral spine. In *T. nodosa*, all five primary spiral cords are usually well developed and bear nodes or tubercles; but in the closely similar *T. meretricula* Röding, 1798, from the central Atlantic islands, the shell surface is covered by very fine spiral sculpture and lacks distinct primary cords. Three tropical American species, the Atlantic *T. deltoidea* (Lamarck, 1822) and the eastern Pacific *T. speciosa* (Valenciennes, 1832) and *T. triangularis* (Blainville, 1832), compose a group in which the fourth primary spiral cord is obsolete or absent. Cords 2, 3, and 5 are adorned with tubercles or nodes. In *Acanthais*, the fifth cord is obsolete or absent, and cords 2 and 3 are adorned with blunt low nodes.

A summary of the distribution of shell-character states in some rapanine general is presented in Table 1. We believe that the combination of traits clearly marks *Acanthais brevidentata* as a rapanine, but sets it apart from the previously named higher taxa in that subfamily.

Shell Microstructure. The shell microstructure shows close

phylogenetic ties with some New World rapanine genera such as *Plicopurpura* and *Vasula*, both of which appear to have the three aragonitic layers and to lack calcite. This structure differs from that of *Acanthina* and other *Ocenebrinae*. *Acanthina unicornis* has one aragonitic layer with a thick calcitic layer (Figure 3B), like that found in most specimens of other *ocenebrines* (*Nucella*, *Forreria*) and *trophonines* (*Trophon*). A double layer of aragonite, as found in some specimens of the latter three genera (Kool, 1993a), was not seen in *Acanthina unicornis*. A single layer of aragonite and a thick layer of calcite also occur in a few "primitive" rapanines, such as *Stramonita*, *Concholepas*, and *Dicathais* (Kool, 1993b).

Operculum. The operculum is similar to that of *Thais*; it is D-shaped and has a lateral nucleus in the center right. In *ocenebrine* genera, the nucleus lies below the center right to the lower right.

Anatomy. The female and male reproductive systems of *Acanthais brevidentata* are very similar to those of, for example, *Thais* and *Rapana*. *Acanthais* lacks a sacklike anterior bursa copulatrix as is present in *Acanthina*, *Nucella*, and *Ocenebra*; furthermore, it has posterior seminal receptacles at the dorsal periphery of the albumen gland, which are absent in *ocenebrines*; and the accessory boring organ and ventral pedal gland share a common duct to the outside, whereas *ocenebrines* have a separate duct for both the ventral pedal gland and the accessory boring organ.

In males of *Acanthais* the prostate is closed, whereas in *ocenebrines* it is open to the mantle cavity posteriorly, and the penis is typically rapanine: sinuous with a vas deferens of the duct-within-a-duct system (Kool, 1988, 1989, 1993a, b).

The accessory salivary glands in *Acanthais* are very short relative to the shell height, whereas *ocenebrines*, such as *Acanthina*, have glands measuring about one-half the shell height. The gland of Leiblein in *Acanthais* is covered by a membrane of interwoven strings of connective tissue; such a membrane is absent in *ocenebrines*. The posterior blind duct of the gland of Leiblein is long (at least one-half of gland length) and opens into the dorsal branch of the afferent renal vein; this duct is very short (less than one-fourth of gland length) in *ocenebrines* and does not reach beyond the posterior buccal cavity.

Radula. The radula of *Acanthais brevidentata* (Figure 4) differs from that of *Acanthina unicornis* (Figure 5) and *Acanthinucella angelica* (Figure 6) in the following ways. The rachidian of *Acanthais* has a wide marginal area with three well-developed marginal denticles and marginal cusp, much as in, for example, *Purpura* and *Drupa* (Kool, 1993b). The rachidian of *Acanthina unicornis* lacks a marginal area, and the base of the serrated outer edge of the lateral cusp connects with the base of a large marginal cusp. Furthermore, it has the bifid edge typical in such genera as *Nucella* and *Ocenebra*, but differs from these in having the central cusp oriented in the same plane as the lateral cusps, rather

Table 1
Distribution of shell-character states among some genera in the Rapaninae.

Character and Character State	Ac	Co	Cy	Ma	Me	Ne	Pl	St	Th	Tl
Central columellar fold										
Present	+		+				+ ¹			+
Absent		+		+	+	+	+ ¹	+	+	
Primary cords on body whorl										
More than 10		+	+							
6 to 7							+			
5	+			+	+	+		+	+	+
Position of cords obsolete on last whorl										
All cords								+ ¹	+ ¹	
Fourth rib									+ ¹	+
First and fifth ribs					+					
Fourth and fifth ribs	+									
None		+		+		+	+	+ ¹	+ ¹	+
Secondary spiral sculpture										
Coarse		+	+				+	+		
Fine to very fine	+			+	+	+			+	+
Adapical notch										
Present			+				+	+ ²		
Absent	+	+		+	+	+		+ ²	+	+
Umbilical slit										
Present						+				
Absent	+	+	+	+	+		+	+	+	+
Liration on outer lip										
Present			+	+	+	+		+		
Absent	+	+					+		+	+
Nodes on spiral cords										
Pointed		+	+	+	+	+	+	+	+	+
Rounded	+									
Absent									+ ¹	
Labral spine										
Basal to all cords		+								
Basal to fifth cord	+						+			
Basal to fourth cord				+						
Absent			+		+		+	+	+	+

Key: Ac *Acanthais*; Co *Concholepas*; Cy *Cymia*; Ma *Mancinella*; Me *Menathais*; Pl *Plicopurpura*; St *Stramonita*; Th *Thais*; Tl *Thalessa*.
+ indicates all member have the character state in question; ¹ indicates that some individuals have the character state in question; ² indicates that members of *Stramonita* s.s. lack, whereas species of the subgenus *Thaisella* Clench, 1947, possess an adapical notch.

than it leaning backward (see Kool, 1993a). The rachidian of *Acanthinucella angelica* bears well-developed outer denticles on a more gently sloping lateral cusp, and has a bifid edge. The radula of *Acanthais* most closely resembles that of *Tribulus planospira* (see Kool, 1993b:fig. 21D); the central cusp of the rachidian tooth of *Acanthais* is much wider relative to the total rachidian width than the same cusp in *Acanthina*. This wide, well-developed central cusp is also present in *Thais nodosa* and *Neorapana muricata* (Kool, 1993b). In its denticulation, however, the *Acanthais* radula closely resembles that of *Stramonita haemastoma* ("floridana").

DISCUSSION

Relationships

Based on the radular and protoconch morphology, the nominal species *brevidentata* could be placed in *Stramonita*. However, the anatomy and shell ultrastructure (in addition to the overall shell morphology) are sufficiently dissimilar between *Acanthais brevidentata* and *Stramonita haemastoma* to warrant separate generic status for the former. *Stramonita* has a large bursa copulatrix in connection with and running alongside the capsule gland, and it has accessory salivary glands that are relatively much longer (one-third

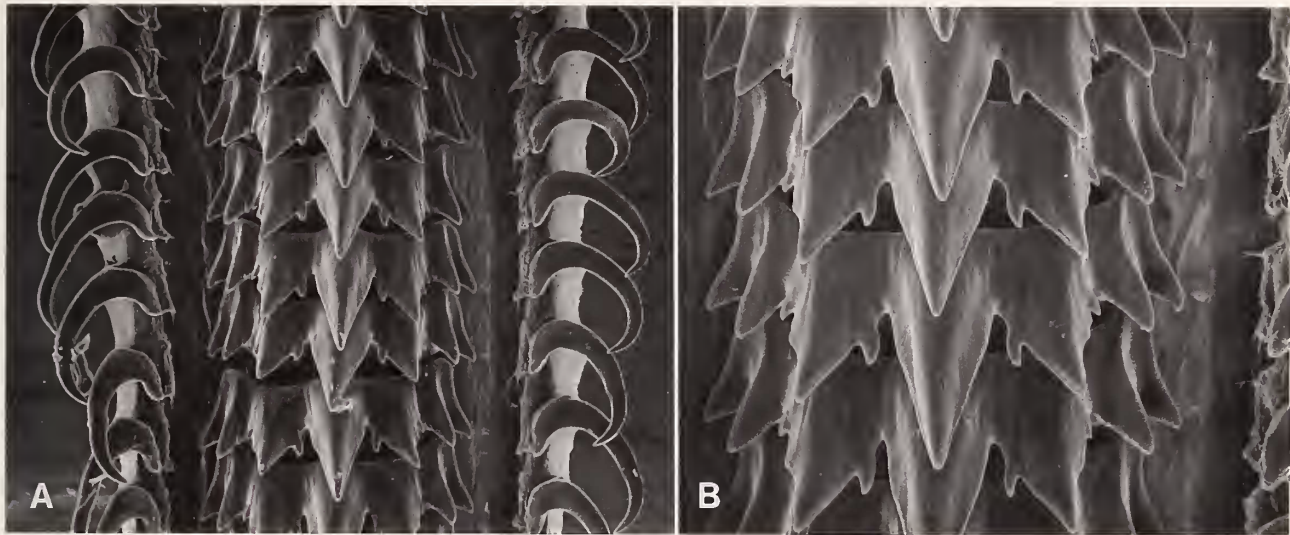


Figure 5

Radula, *Acanthina unicornis*, Talcahuano, Chile, MCZ 3717. A. $\times 450$. B. rachidian tooth, $\times 700$.

of shell height) than those in *Acanthina*. In addition to the differences in external shell morphology mentioned previously in this paper, *Stramonita* has a thick calcitic layer and one or two aragonitic layers.

From examination of an extensive suite of morphological characters taken from external shell morphology, protoconch, shell ultrastructure, operculum, anatomy, and radula, it is evident that *Acanthina brevidentata* should be taken out of the ocenebrine genus *Acanthina* and should be given a new generic name and placed in the Rapaninae (Thaidinae of authors; see Kool, 1993b).

Using characters of anatomy, protoconch, and shell microstructure, Kool (1993b) constructed a phylogenetic hypothesis of relationships in the Rapaninae. Incorporation into his analysis of results reported here for *Acanthais* shows that the latter taxon belongs to Kool's Clade G, which includes *Thais*, *Vasula*, *Neorapana*, *Tribulus*, *Mancinella*, and *Purpura*. Relationships within this clade were not resolved by Kool (1993b), but evidence offered in the next section implies that labral spines have evolved three times independently within Kool's Clade G (in *Acanthais*, *Mancinella*, and *Neorapana*).

We have chosen to propose the new genus *Acanthais* because the type species, *A. brevidentata*, does not readily fit into any named rapanine genus. An alternative solution would be to employ a single large genus *Thais* or *Purpura* for members of Clade G. Such a solution would, we believe, obscure relationships among distinct rapanine taxa. Regardless of whether *Acanthais* is accepted as a valid genus, the conclusion that it belongs to the Rapaninae and not to the genus *Acanthina* in the Ocenebrinae is strongly supported by an analysis of shell and anatomical characters.

Evolution of Labral Spines Within the Rapaninae

Short basal labral spines have evolved at least five times independently within the subfamily Rapaninae. They occur in *Acanthais* and *Neorapana* from the tropical eastern Pacific, *Concholepas* of the temperate southeastern Pacific, *Mancinella alouina* of the tropical Indo-Pacific, and several Indo-Pacific Miocene species of *Taurasia* Bellardi, 1882 (type species: *T. subfusiformis* (Orbigny, 1852), Miocene of southern Europe). The position of the spine is the same (basal to the fifth primary spiral cord) in *Acanthais* (Figure 1) and *Neorapana*, but differences in shell morphology and

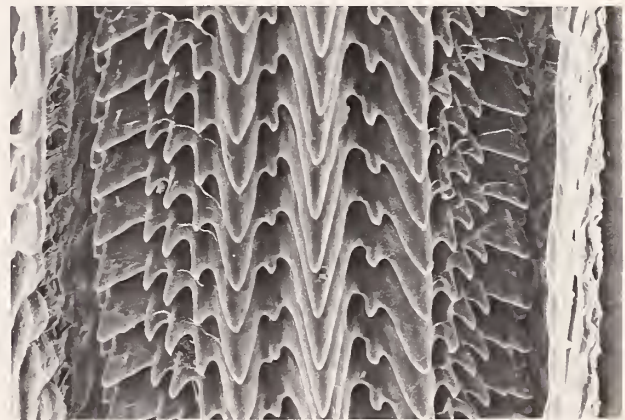


Figure 6

Radula, *Acanthinucella angelica*, $\times 900$.

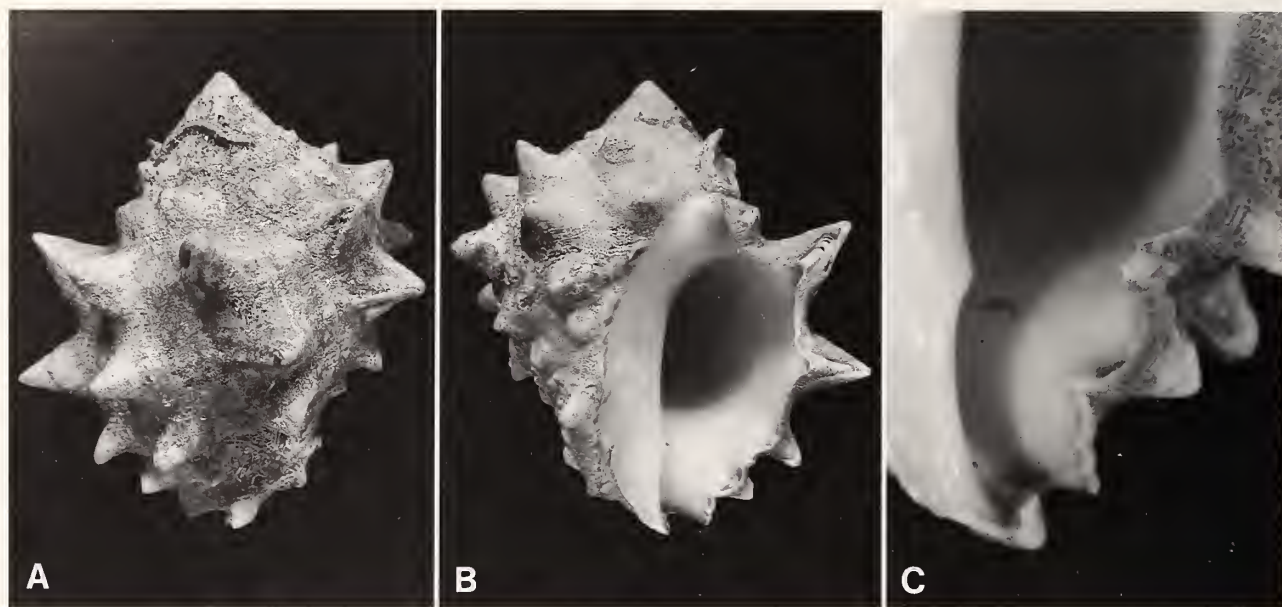


Figure 7

Shell morphology, *Mancinella alouina*, Nossy Komba, Madagascar, collected 27 June 1972. A. dorsal view, $\times 1.5$. B. apertural view, $\times 1.5$. C. basal portion of outer lip, $\times 4$.

anatomy discussed above imply that the labral spine evolved independently in these two genera. *Mancinella alouina* has the spine situated between the fourth and fifth primary cords (Figure 7), and is therefore likely to have evolved its spine independently of *Acanthais* and *Neorapana*. Some individuals of *M. alouina* lack a labral spine, as do other Indo-Pacific species of *Mancinella*. In *Concholepas*, the labral spine is very blunt, and usually consists of two adjacent protrusions instead of only one. This genus is phylogenetically close to the Australian and New Zealand genus *Dicathais* Iredale, 1936 (type species: *D. orbita* (Gmelin, 1791)) and is not close to the three genera mentioned previously (see Kool, 1993b).

Several Miocene species of the unusual genus *Taurasia* from Indonesia and the Philippines have a labral spine and an umbilical slit (see Beets, 1984, for a taxonomic review). The single living representative, *T. buccinea* (Deshayes, 1844), lacks a labral spine and has not been examined anatomically. Shell characters, including a parietal rib, place it in the Rapaninae, perhaps close to genera such as *Morula* Schumacher, 1817 (type species: *M. uva* (Röding, 1798), tropical Indo-Pacific) and *Muricodrupa* Iredale, 1918 (type species: *M. fenestrata* (Blainville, 1832), tropical Indo-Pacific); and *Cronia* H. & A. Adams, 1853 (type species: *C. amygdala* (Kiener, 1835), tropical Indo-Pacific). These genera have often been placed in the subfamily Ergalataxinae, but Kool (1993b) has shown that they form a clade within the Rapaninae. *Taurasia* has a straight columella with one or two central folds and several

riblets basal to it. The outer lip is lirate within, and its apical end is extended as a gutter opposite the parietal tubercle. External sculpture consists of axial folds (sometimes confined to the early whorls) crossed by many scaly primary and secondary spiral ribs. Whatever the correct placement of *Taurasia*, it is clear that the labral spine evolved independently in this genus from the other four genera discussed above.

Labral spines in the Rapaninae are enlarged crenations on the edge of the outer lip that project ventrally more than do the other crenations. The tendency for one or more crenations on the basal part of the outer lip to be enlarged and to protrude ventrally is very widespread among members of the subfamily. It is well exemplified in several species of *Stramonita*, including the eastern Pacific *S. biserialis* (Figure 8), eastern Atlantic populations of *S. haemastoma*, and the Indo-Pacific *S. bitubercularis* (Lamarck, 1822). The enlarged crenations, which are often set off from the more adapical crenations by a space, are at the same position on the outer lip as is the labral spine of *Acanthais* and *Neorapana* (basal to the fifth cord). Some specimens of *Acanthais brevidentata* from throughout the geographic range of that species have an arrangement of crenations similar to that in species of *Stramonita* mentioned above, but one of the crenations is typically a little larger than the others and is equivalent to a poorly expressed labral spine. Other examples of enlarged and ventrally more projecting basal crenations occur in *Cronia avellana* (Reeve, 1846) and *Morula marginalba* (Blainville, 1832) from Aus-

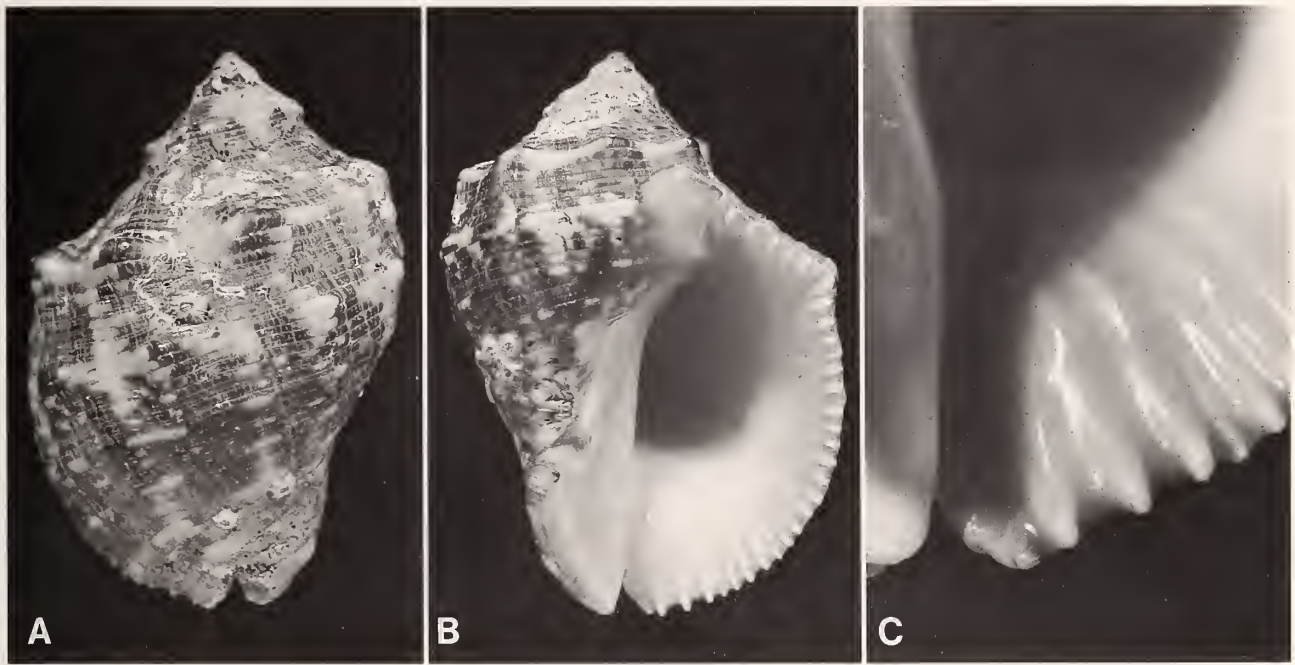


Figure 8

Shell morphology, *Stramonita biserialis*, Punta Caldera, Costa Rica, collected 3 July 1973. A. dorsal view, $\times 1.5$. B. apertural view, $\times 1.5$. C. basal portion of outer lip, $\times 4$.

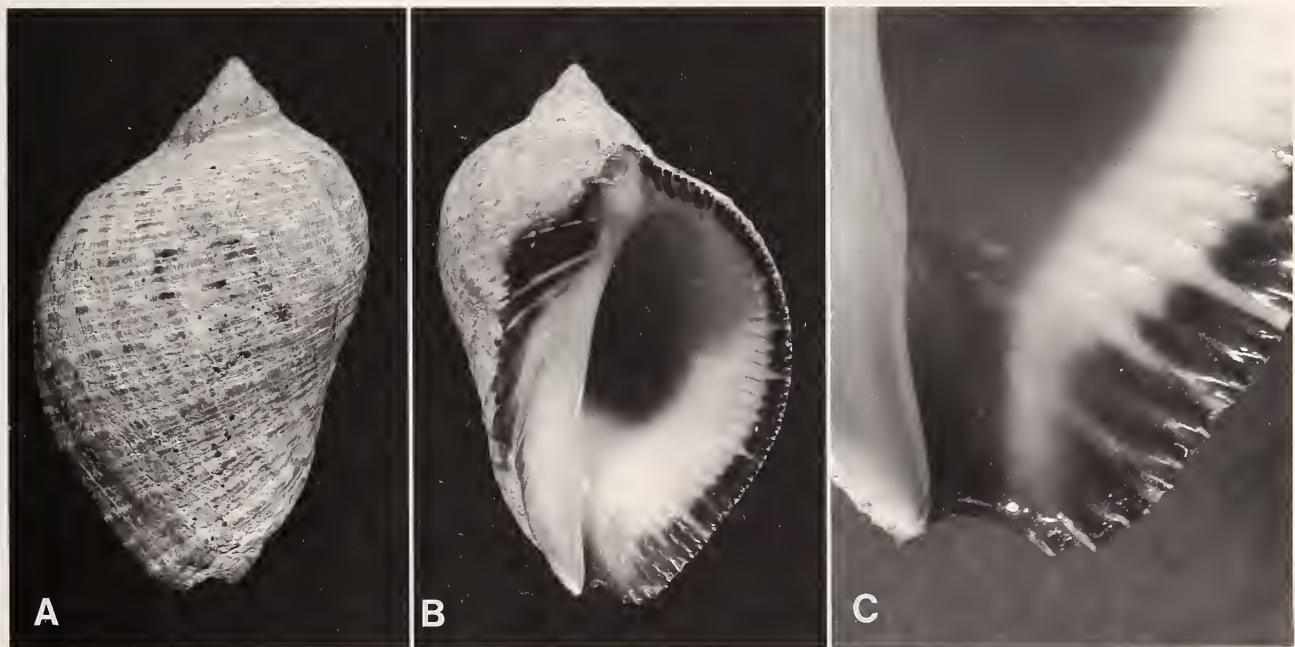


Figure 9

Shell morphology, *Purpura persica*, Guguan Island, Northern Marianas, collected 14 July 1981. A. dorsal view, $\times 1.5$. B. apertural view, $\times 1.5$. C. basal portion of outer lip, $\times 4$.

tralia, *Muricodrupa fenestrata* from the Indo-Pacific, *Thaisella lacera* (Born, 1778) from the Indian Ocean, and species of *Rapana* and *Purpura* Bruguière, 1789 (type species: *P. persica* (Linnaeus, 1758)) from the western Pacific (Figure 9). The labral spine is thus merely an exaggerated crenation, and it is not surprising that such a feature has evolved repeatedly and in the same position on the outer lip in several clades in the subfamily.

Given their identical positions on the outer lip basal to the fifth primary spiral cord, the labral spines of *Acanthais* and *Neorapana* are homologous. A superficial analysis would support a single evolutionary origin of this feature, but evidence from other characters indicates that the evolution of labral spines is parallel in the two genera. This case illustrates well the potential pitfalls of a superficial character analysis in phylogenetic reconstruction.

Biogeographical Remarks

Acanthais is one of at least nine endemic tropical eastern Pacific genera or species groups of common rocky-shore gastropods with no known living or fossil members outside the Panamic Province. These include the trochid *Tegula* Lesson, 1830; the turbinids *Callopoma* and *Uvanilla*, both of Gray, 1850; the muricids *Neorapana*, *Muricanthus* Swainson, 1840, and *Vasula* Mörch, 1860; the fascioliariid *Opeatostoma* Berry, 1958; and the siphonariid *Heterosiphonaria* Hubendick, 1945. Vokes (1990) considered *Muricanthus* to be a synonym of *Hexaplex* Perry, 1810 on the basis of the strong resemblance between the three eastern Pacific species of the group and the type species of *Hexaplex*, *H. cichoreum* (Gmelin, 1791) from the Indo-Malayan region of the Indo-Pacific. The three species of *Muricanthus* differ from all related species of *Hexaplex* in the New World and West Africa by the presence of a labral protrusion, and probably represent convergence in this character with the Indo-Pacific species such as *H. cichoreum* and *H. kusterianus* (Tapparone-Canefri, 1875). They therefore compose a distinctive endemic eastern Pacific clade. No fossil record is known for *Tegula*, *Acanthais*, *Opeatostoma*, or *Heterosiphonaria*. The other endemic groups are known back to the early Miocene (*Vasula*) or Early Pliocene (the other four genera) (see Durham, 1950; Woodring, 1959; Emerson & Hertlein, 1964; Vokes, 1990). Although the possibility that these groups once occurred in the western Atlantic cannot be ruled out, the available evidence indicates that significant genus-level evolution has taken place in the eastern Pacific since the uplift of the Isthmus of Panama during the Pliocene. It is striking that four of the groups (*Acanthais*, *Muricanthus*, *Neorapana*, and *Opeatostoma*) have evolved a labral spine. None of the western Atlantic relatives of these genera possesses such protuberances. These facts imply that evolutionary conditions in the eastern Pacific after the uplift of the isthmus have been very different from those in the western Atlantic.

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